Size Composition of Prey in the Orb-Web Spider *Nephila clavata* Estimated by Video Recordings and Sight-Count Censuses

Tadashi MIYASHITA[1]

宮下　直[1]：ジョロウグモの餌サイズ構成のビデオ記録と見取り
センサスによる推定

Abstract　Size composition of prey by number and feeding time was estimated in the orb-web spider *Nephila clavata* by means of video recordings and sight-count censuses. Small prey ($\leqq 2$ mm in body length) constituted more than 80% by number and nearly 30% of feeding time. Distributions of prey size in terms of feeding time were similar between the two methods. Considerable variation in feeding time was found among individuals, but the small prey were eaten relatively constant. The significance of small prey and reasons for wide range utilization of prey size in web-building spiders are discussed.

Introduction

Prey size selection is an important aspect of foraging strategy for predatory animals. Classical optimal foraging theory predicts that predators should capture the most profitable prey, *i.e.*, the highest ratio of energy gain to unit foraging time. In nature, however, the encounter rate of profitable prey may be low and unpredictable, which may broaden the range of prey size that predators capture. MACARTHUR (1972) proposed that large animals eat various size of prey because they encounter prey of suitable size much less frequently than small animals that rely on small prey. This phenomenon is known in spiders: the range of prey size increases with the growth of spiders (*e.g.*, MURAKAMI, 1983; TANAKA, 1991).

Size composition of prey in spiders has been often examined in terms of number (*e.g.*, UETZ *et al.*, 1978, NENTWIG, 1980, 1985; MURAKAMI, 1983) but rarely estimated by weight (OLIVE, 1980). To compare the relative importance of prey in different size classes, estimation of prey weight is essential, since it will contribute to growth and reproduction more directly than number of prey. In the present paper I estimated number and feeding time of prey in different size classes in the spider *Nephila clavata* by means of video recordings and sight-count censuses, because feeding time approximately reflects amount of food

1) Laboratory of Forest Zoology, Faculty of Agriculture, University of Tokyo, Bunkyo-ku, Tokyo, 113 Japan
東京大学農学部森林動物学教室

ingested and it can be measured relatively easily in the field.

Materials and Methods

Video recordings of spider feeding activity were conducted in the Tokyo University Forest Experimental Station in Tanashi, Tokyo. Spiders inhabiting the forest edge near the research building were the study subjects. Most of them were adult females with the mean body length 16.6±2.6 (SD)mm (n=27). Twenty-two spiders were recorded by a video camera from September 7 to October 24, 1989. Each recording time ranged from 2 to 6 hours duration taken between 11:30 and 17:00. The video camera (SONY, CCD-V88) was set at an appropriate position from which a spider handling prey with her chelicerae could be identified. The distance from the spider to the camera lens was about 120 cm. In 1991, 5 spiders were recorded from September 24 to October 19. Methods for recording were the same as those in 1989. Recording time over the two years totaled 6,246 minutes. Video cassettes were replayed on a television screen and the following feeding events were recorded: initiation and termination of feeding on prey, prey body length (nearest mm), and prey taxon. Termination of feeding on small prey was rather difficult to identify because spiders seem to consume the whole prey body without discarding prey remains. Close observations revealed that chelicerae of spiders moved intermittently while feeding on prey, so I regarded the moment when no movement of chelicerae was observed as the termination of feeding.

Sight-count censuses were performed in 1989 at the same site as the video recording. From September 7 to October 14, one to three censuses per day (a total of 26 days) were made with an interval of at least 2 hours. A total of 557 spider-censuses were conducted. When spiders held prey with their chelicerae, prey body length and taxon were recorded.
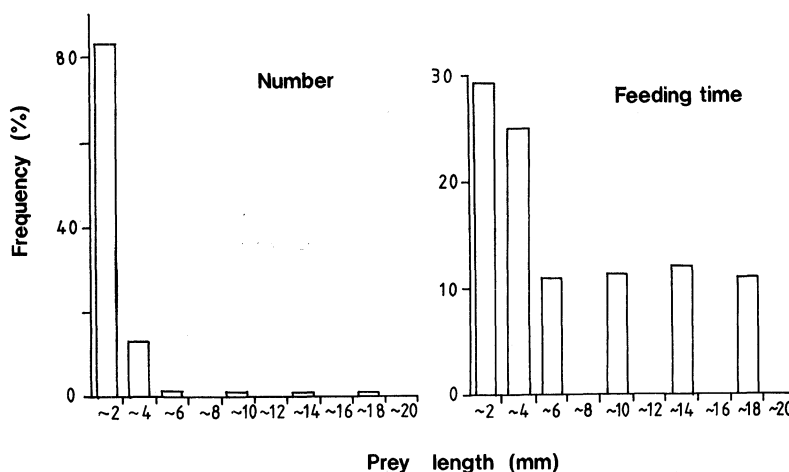

Fig. 1. Prey size distribution of *Nephila clavata* estimated by video recordings. Total number of prey 128, and total feeding time 1,451 min.

Percentage contribution of prey in a particular size class to the total feeding time was estimated as follows. Let us assume that handling time of prey with size i is given by t_i. Then, the percentage of feeding time of prey with size $i(P_i)$ is expressed as,

$$P_i = \frac{n_i t_i}{\Sigma \, n_i t_i} \times 100$$

where n_i is the number of prey with size i eaten by the spider during a given period. This value is equivalent to the probability that a prey observed at a particular census belongs to the size class i. Hence, P_i is also obtained by the following simple calculation using sight-count data, P_i = (no. observed feeding on prey with size i) × 100 / (total no. observed feeding) [equation (1)].

Results

During 6,246 minutes of video recording, 128 prey were fed on by spiders and their total feeding time was 1,451 minutes. Small prey up to 2 mm were most numerous, constituting more than 80% of total prey, while prey larger than 4 mm were very rare (Fig. 1, left). With regards to feeding time, prey of the smallest class were also most common (nearly 30%) but to a lesser extent than that by number (Fig. 1, right). Relatively large size classes often showed more than 10% of the total in feeding time.

Figure 2 shows individual variation in percentage of feeding time to the total recording time. Only individuals that were recorded continuously for more than 4 hours were used. Considerable variation was found among individuals, which was caused mainly by large prey. In the largest size class, even a single prey occupied more than 50% of the total recording time. Contribution of small prey was fairly low, being less than 20% in most instances. However, small prey were always eaten and their variation in feeding time seemed to be small compared to that of large prey.

Size composition of prey in terms of feeding time was estimated by the sight-count method, using equation (1). The distribution was similar to that
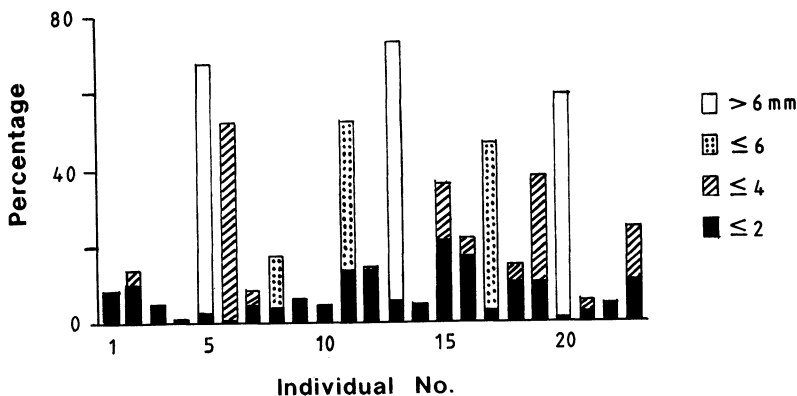

Fig. 2. Individual variation in the proportion of feeding time on different prey size classes to the total recording time.
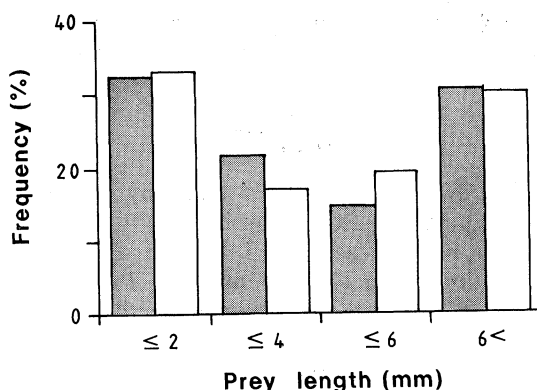
Fig. 3. Prey size distribution in terms of feeding
time of *Nephila clavata* estimated by video
recordings (hatched bars) and sight-count
censuses (open bars) in 1989. Total feeding
time 1,061 min and total number of prey
counts 87.

estimated by the video camera in 1989 (Fig. 3) and no statistical difference
was detetced ($\chi^2 = 1.17$, $p = 0.759$).

Taxonomic composition of prey in terms of feeding time estimated by the
sight-count census was as follows. Hymenoptera, 21.8%: Diptera, 13.8%:
Homoptera, 11.5%: Coleoptera, 5.8%: Lepidoptera, 2.3%: other orders, 4.6%:
Unidentified, 40.2%. Most homopterans were winged aphids and most hymenop-
terans were bees and wasps. Unidentified items were well-macerated prey.
Identification by video recording was extremely difficult for small prey, so no
data is shown here.

Discussion

Size distribution of prey in terms of number for *N. clavata* was highly
skewed to small prey, and mean prey length was 1.95 mm (Fig. 1). This result
is quite different from most of other studies dealing with orb-weavers in that
prey size is smaller in *N. clavata* (Uetz *et al.*, 1978; Olive, 1980; Uetz and
Biere, 1980; Murakami, 1983). However, Nentwig (1985) showed size
compositions similar to the present result: number of small prey (≤ 2 mm) con-
stituted 60–70% in the diet of *Nephila* and *Argiope* spiders, and mean prey
lengths were 2.1–2.8 mm. As Nentwig pointed out, sampling in most studies
are biased to large prey, because only discarded prey remains or enwrapped
prey were sampled. Nentwig counted the number of all prey on the web, since
small insects left on the web are consumed later when spiders eat the old thread
(Peakall, 1964.) However, his method may underestimate prey which were
immediately attacked (*i.e.*, large prey) because these prey must have been already
consumed and discarded by the spider before sampling, which leads to over-

estimation of relative contribution of small prey. The method used in the present paper ignores the prey left on the web and hence the percentage contribution of small prey may be underestimated, but not to the degree of other studies since I recorded all prey items actually eaten by spiders. Despite differences in methods, study sites and species between the paper of NENTWIG and the present study, prey size distribution showed a similar pattern. Since these two studies employed stricter methods compared to others, the results may more closely reflect actual prey composition of orb-weavers.

From the energetic viewpoint, prey size distribution in terms of feeding time seems to be a more meaningful measure for spiders than number of prey, since feeding time may be proportional to food consumption and hence may influence growth and reproduction. Contribution of small prey (≤ 2 mm) was nearly 30%, which was the highest of all size classes (Fig. 1). Results obtained by the two methods, *i.e.*, video recording and sight-count census, were very similar (Fig. 3), which strengthens the reliability of my estimates. OLIVE (1980) demonstrated quite different prey size distributions by dry mass in *Argiope trifasciata* and *Araneus trifolium* compared to the present study. Taht is, for prey less than 8–9 mm, biomass contributed to diet increased with prey length. Since his estimate was made by observing spiders continuously for several hours, methodological differences between these two studies are small. Thus, species differences and/or site differences must be involved. Small mesh size in webs of *N. clavata* may be the cause for the large proportion of small prey in this species.

Video recordings clarified great spatio-temporal variation in foraging success among individuals, which was caused mainly by large prey (Fig. 2). In general, number of insects in a habitat decreased exponentially with their body size (NENTWIG, 1985, 1989, MIYASHITA, 1990). It is therefore not surprising that small prey are captured frequently and large ones captured rarely. I often observed that *N. clavata* picked up small prey attached to the web when large prey were not available. Although the contribution of small prey by biomass is not very large, it may reduce the risk of starvation, since small prey are available at any time.

One reason why web-building spiders utilize wide range in prey size may be due to low encounter rate with profitable prey, as proposed in other predators (*e.g.*, KREBS and DAVIES, 1991). Another reason may come from the unique prey capture method. Once a web is built, many small insects are necessarily captured and glued to the web, even if the web is designed to capture large prey. Thus, spiders can eat small prey with little additional energetic costs. It appears that the habit of filter feeding enables web-building spiders to exploit prey size of a broad range.

Acknowledgments

摘　　要

　ジョロウグモの餌の捕獲個体数と摂食時間に関するサイズ構成を，ビデオによる記録お
よび見取りセンサスにより推定した．体長 2 mm 以下の小型餌は，個体数では 80% 以
上，摂食時間では約 30% を占めていた．摂食時間についての餌サイズ構成は，2つの方
法で大変似かよっていた．摂食時間の個体間での変異は大きかったが，小型の餌は比較的
コンスタントに摂食されていた．小型餌の重要性と，造網性クモにおける幅広い餌サイズ
の利用の理由に関して考察を行った．

References

KREBS, J. R., & N. B. DAVIES, 1991. Behavioural Ecology: an evolutionary approach, 3rd
　　edn. 482 pp. Blackwell Scientific Publications, Oxford.
MACARTHUR, R. H., 1972. Geographical Ecology: patterns in the distribution of species.
　　269 pp. Harper & Row, New York.
MIYASHITA, T., 1990. Decreased reproductive rate of the spider, *Nephila clavata*, inhabiting
　　small woodlands in urban areas. *Ecol. Res.*, **5**: 341–351.
MURAKAMI, Y., 1983. Factors determining the prey size of the orb-web spider, *Argiope
　　amoena* (L. KOCH) (Argiopidae). *Oecologia*, **57**: 72–77.
NENTWIG, W., 1980. The selective prey of linyphiid-like spiders and of their space webs.
　　Oecologia, **45**: 236–243.
———— 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae:
　　Araneidae) and a comparison with araneids of temperate zone. *Ibid.*, **66**: 580–594.
———— 1989. Seasonal and taxonomic aspects of the size of arthropods in the tropics and
　　its possible influence on size-selectivity in the prey of a tropical spider community.
　　Ibid., **78**: 35–40.
OLIVE, C., 1980. Foraging specializations in orb-weaving spiders. *Ecology*, **61**: 1133–1144.
PEAKALL, D., 1964. Composition, function and glandular origin of the silk fibroins of the
　　spider *Araneus diadematus* Cl. *J. Exp. Zool.*, **156**: 345–350.
TANAKA, K., 1991. Food consumption and diet composition of the web-building spider
　　Agelena limbata in two habitats. *Oecologia*, **86**: 8–15.
UETZ, G., & M. BIERE, 1980. Prey of *Micrathena gracilis* (WALCKENAER) (Araneae:
　　Araneidae) in comparison with artificial webs and other trapping devices. *Bull. Br.
　　arachnol. Soc.*, **5**: 101–107.
————, A. JOHNSON, & D. SCHEMSKE, 1978. Web placement, web structure, and prey
　　capture in orb-weaving spiders. *Bull. Br. arachnol. Soc.*, **4**: 141–148.